

A TAXONOMIC ASSESSMENT OF *Bartramia*, *Breutelia* AND *Exodokidium* ON SOUTH GEORGIA

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ABSTRACT. A statistical representation, combined with a discriminatory assessment of taxonomic characters, has shown that *Bartramia patens* Brid., *Bartramia subsymmetrica* Card. and *Breutelia integrifolia* (Tayl.) Jaeg. occur on South Georgia, and are the only known representatives of these genera on the island. Their taxonomic limits have been defined and compared with type material. *Bartramia leucolomacea* C. Muell., *B. oreadella* C. Muell., *B. oreadella* var. *microphylla* Card., *B. pycnocolea* C. Muell., *B. leucocolea* Card. and *B. leucocolea* var. *brevifolia* Broth. & Card. are shown to be synonymous with *B. patens*. A record of *B. diminutiva* C. Muell. on South Georgia is shown to be erroneous. *Exodokidium subsymmetricum* (Card.) Card. is transferred to the genus *Bartramia* as *B. subsymmetrica* Card., and *Bartramia mniocarpa* C. Muell. (non *Bartramia mniocarpa* Schimp. *nom. nud.*) is reduced to synonymy with *Breutelia integrifolia*.

CONFUSION in the taxonomy of *Bartramia* on South Georgia has long been recognized. Cardot (1908), for example, suggested that four species, *B. diminutiva* C. Muell., *B. oreadella* C. Muell., *B. pycnocolea* C. Muell. and *B. subpatens* C. Muell., could be regarded as forms of the polymorphic species *B. patens* Brid., and he reduced *B. subpatens* to varietal status as *B. patens* var. *austrogeorgica* Card. Moreover, he considered that plants defined as *B. leucolomacea* C. Muell. might also be properly placed in *B. patens*. Thus he was of the opinion that the only valid species known on South Georgia were *B. leucocolea* Card. and *B. patens*, although he continued to recognize six species, two varieties, *B. oreadella* var. *microphylla* Card. and *B. leucocolea* var. *brevifolia* Broth. & Card., and three forms of *B. patens*, f. *austrogeorgica* Card., f. *chrysocolea* Card. and f. *fragilifolia* Card. Dixon (1920) later upheld Cardot's view of *B. diminutiva*, as well as of *B. pycnocolea* (Dixon, 1935), but these species were included in Steere's (1961) check list and no further reduction to synonymy has since been made. The present study was, therefore, carried out in an attempt to define taxonomic limits both within and between the two closely related genera, *Bartramia* and *Exodokidium*, the latter being represented on South Georgia by a single species, *E. subsymmetricum* (Card.) Card. A similar investigation was made of *Breutelia kerguelensis* (Par.) Wijk & Marg., the only species of this genus reported from South Georgia.

MATERIALS AND METHODS

A total of 543 specimens from the British Antarctic Survey herbarium was examined, together with a small number from those herbaria mentioned in the text which also loaned type material. Full descriptions of the species recognized have been given elsewhere (Newton, in press).

As pointed out by Dixon (1924), diagnostic characters in the Bartramiaceae are drawn almost exclusively from the gametophyte, and this is particularly true of the South Georgian species of *Bartramia* and *Breutelia*, although a sporophytic character contributes to the distinction between *Bartramia* and *Exodokidium*.

All the South Georgian species of *Bartramia* belong to the Vaginella section of the genus and, in common with *Exodokidium subsymmetricum*, have clearly defined sheathing leaf bases, more or less suddenly contracted into narrower limbs, which taper to acute apices. Characters that would give some indication of the relative length of base and limb, compared with their individual size and shape, were therefore selected for study (Table I). The basal part of the leaf in *Breutelia*, however, is only sub-sheathing, and is less distinct. The shape varies from ovate to ovate-lanceolate, and the only two ratios considered in this case were intended as measures of overall leaf shape. In each instance an attempt was made to correlate leaf dimensions with other gametophyte and sporophyte characters.

Moving means of leaf dimensions calculated for a randomly selected specimen of each genus showed that 25 leaves, five from each of five stems, would provide an adequate sample, and this was subsequently adopted as a standard throughout the study. Similarly, leaf-cell length was satisfactorily represented by the measurement of five cells from about half-way along the

TABLE I. LEAF CHARACTERS ASSESSED FOR THE SOUTH GEORGIAN SPECIES OF *Bartramia*, *Breutelia* AND *Exodokidium*

Characters	<i>Bartramia</i>	<i>Breutelia</i>	<i>Exodokidium</i>
Limb length (<i>a</i>)	+	+	+
Limb breadth at base	+	-	+
Limb ratio, length/breadth	+	-	+
Base length (<i>b</i>)	+	+	+
Base breadth at widest point (<i>c</i>)	+	+	+
Base ratio, length/breadth	+	-	+
Limb/base ratio (<i>a/b</i>)	+	+	+
Total leaf length (<i>a + b</i>)	+	+	+
Leaf length/breadth ratio (<i>a + b/c</i>)	+	+	+
Leaf-cell length	+	+	+
Leaf-cell breadth	+	+	+

+ Indicates that the character was assessed for the genus indicated.

- Indicates that no assessment was made.

limb in each of five leaves taken from separate stems. Leaf-cell breadth was found to be less variable, however, and one measurement from each of the above five leaves proved adequate.

VARIATION IN *Bartramia* AND *Exodokidium*

Leaf dimensions

Scatter diagrams based on data obtained from 118 randomly chosen specimens of *Bartramia* and *Exodokidium* revealed that marked discontinuity of variation does not occur in any of the characters investigated. Nevertheless, Figs. 1, 2 and 3 represent asymmetrical distributions of variation, and thus differ from the patterns which might be expected from bivariate normal distributions if the material belonged to a single taxon. In the majority of specimens, leaf length showed a strong positive correlation with base breadth, but a few of those with short leaves had broader bases than is consistent with the main body of data (Fig. 1). Conversely, Fig. 2 indicates that leaf length and the base ratio (length/breadth) are probably generally uncorrelated, yet it is apparent that there is a small number of specimens distinguished by their comparatively low base ratios. Leaf-cell length when compared with the limb ratio (length/breadth) was similarly found to isolate a small group of plants with short cells and low limb ratios (Fig. 3). In passing it may be noted that cell length was the only character which showed any tendency, albeit slight, to discriminate between representatives of the main part of the variation.

It became apparent that the small number of specimens separated from the main group by these means was the same in each instance, and that most of them conformed to Cardot's (1906, 1908) description of *Exodokidium subsymmetricum*, particularly in growth form and vegetative morphology. That the distinguishing character was invariably directly related to breadth was also immediately evident and reference to Fig. 4 emphasizes the continuous variation throughout the range of material in other characters such as limb length in relation to the length of the base. It would seem unwise to recognize a taxon of generic or even specific rank on a single variable that showed incomplete discontinuity. A detailed examination was therefore made of a number of other characters, including those which have been considered to discriminate between *Bartramia* and *Exodokidium*, to see if correlations could be found with any other characters to separate the two groups, which for convenience will be referred to as the *Exodokidium* group (small group) and the *Bartramia* group (large group).

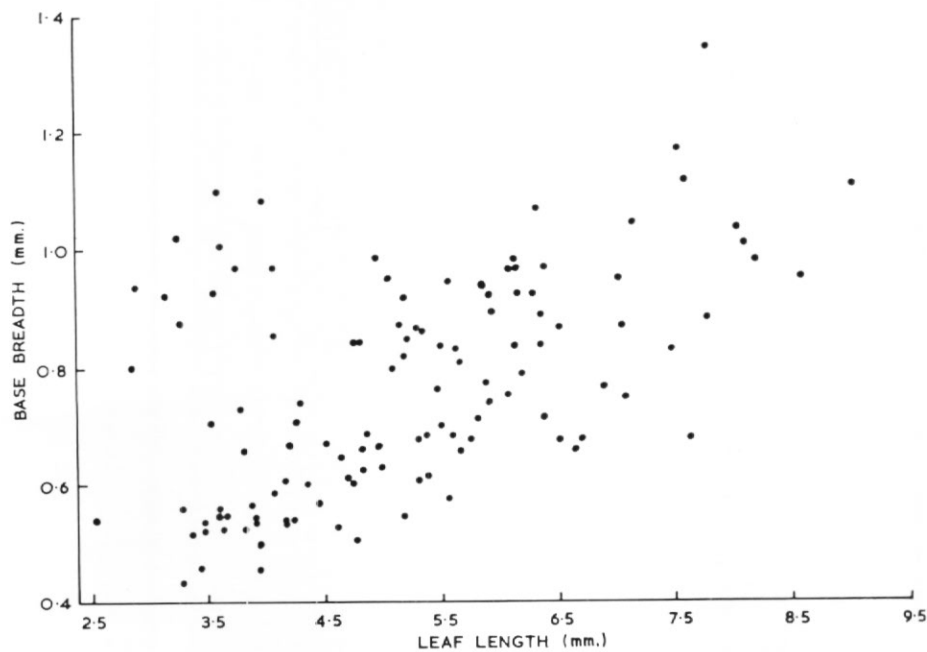


Fig. 1. Scatter diagram of variation in base breadth and leaf length in South Georgian specimens of *Bartramia* and *Exodokidium*.

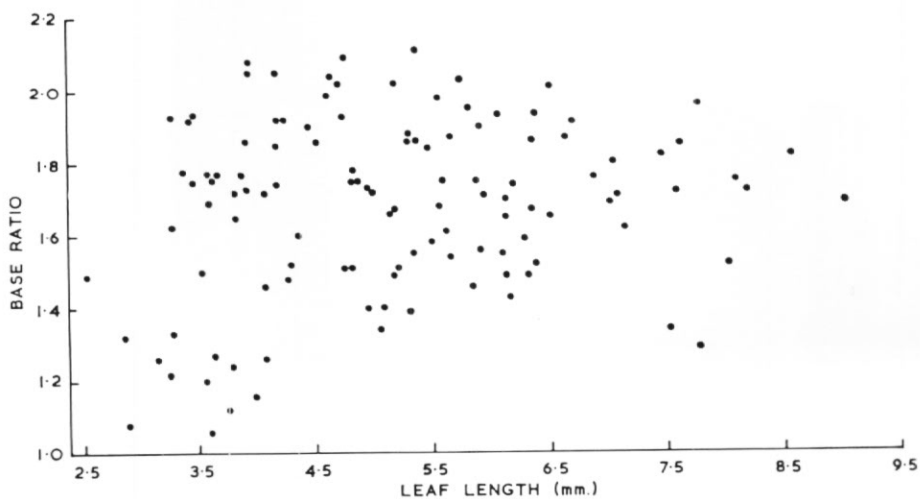


Fig. 2. Scatter diagram of variation in base ratio (length/breadth) and leaf length in South Georgian specimens of *Bartramia* and *Exodokidium*.

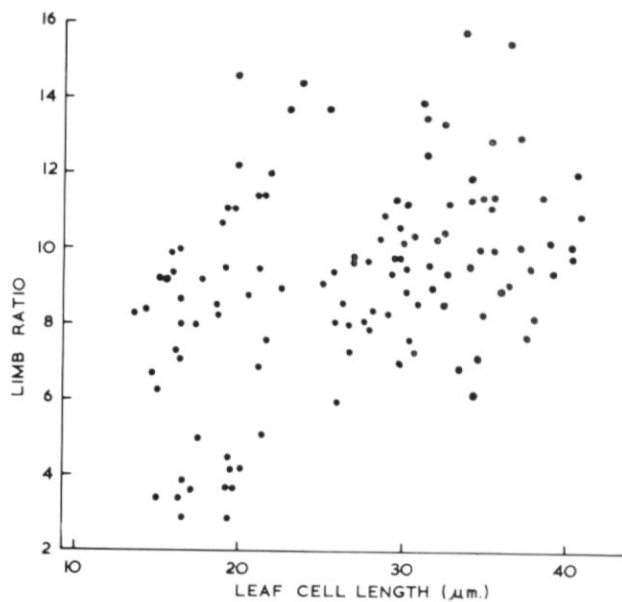


Fig. 3. Scatter diagram of variation in limb ratio (length/breadth) and leaf-cell length in South Georgian specimens of *Bartramia* and *Exodokidium*.

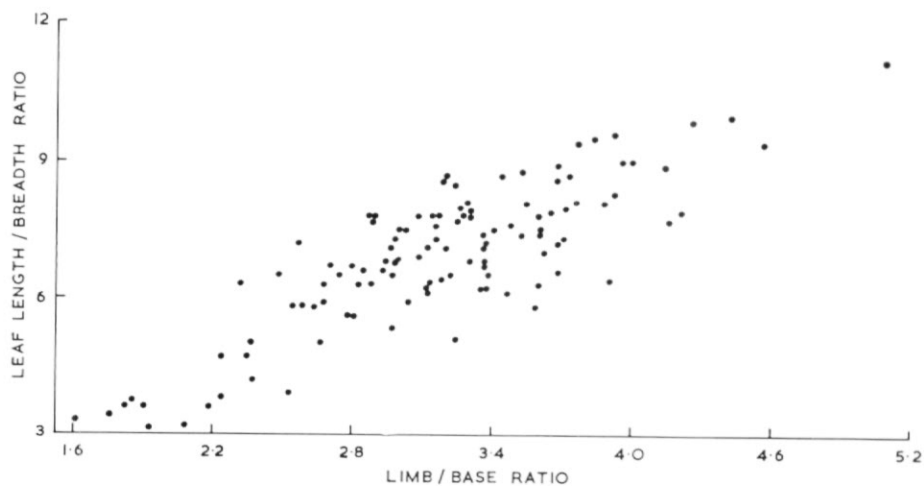


Fig. 4. Scatter diagram of variation in leaf length/breadth ratio and ratio of limb/base (a/b ratio) in South Georgian specimens of *Bartramia* and *Exodokidium*.

Leaf and stem sections

The sheathing leaf bases of plants of both the *Exodokidium* and *Bartramia* groups are similar, each having a nerve that is not more than one-fifth the width of the leaf, and a lamina composed of a single layer of thin-walled cells, although scattered bi-seriate points also occur. The tapering leaf apices are also indistinguishable, being triangular in transverse section, and composed almost entirely of small incrassate cells. Sections taken approximately half-way along the leaf limb, however, show distinct differences in nerve structure between the two groups (Fig. 5a-c). The lamina in both groups is tri-seriate to within a few rows of the margin, where it is usually bi-seriate, although one or two rows of a single cell thickness are occasionally present. The mid-point of the leaf is thicker and usually plano-convex in section,

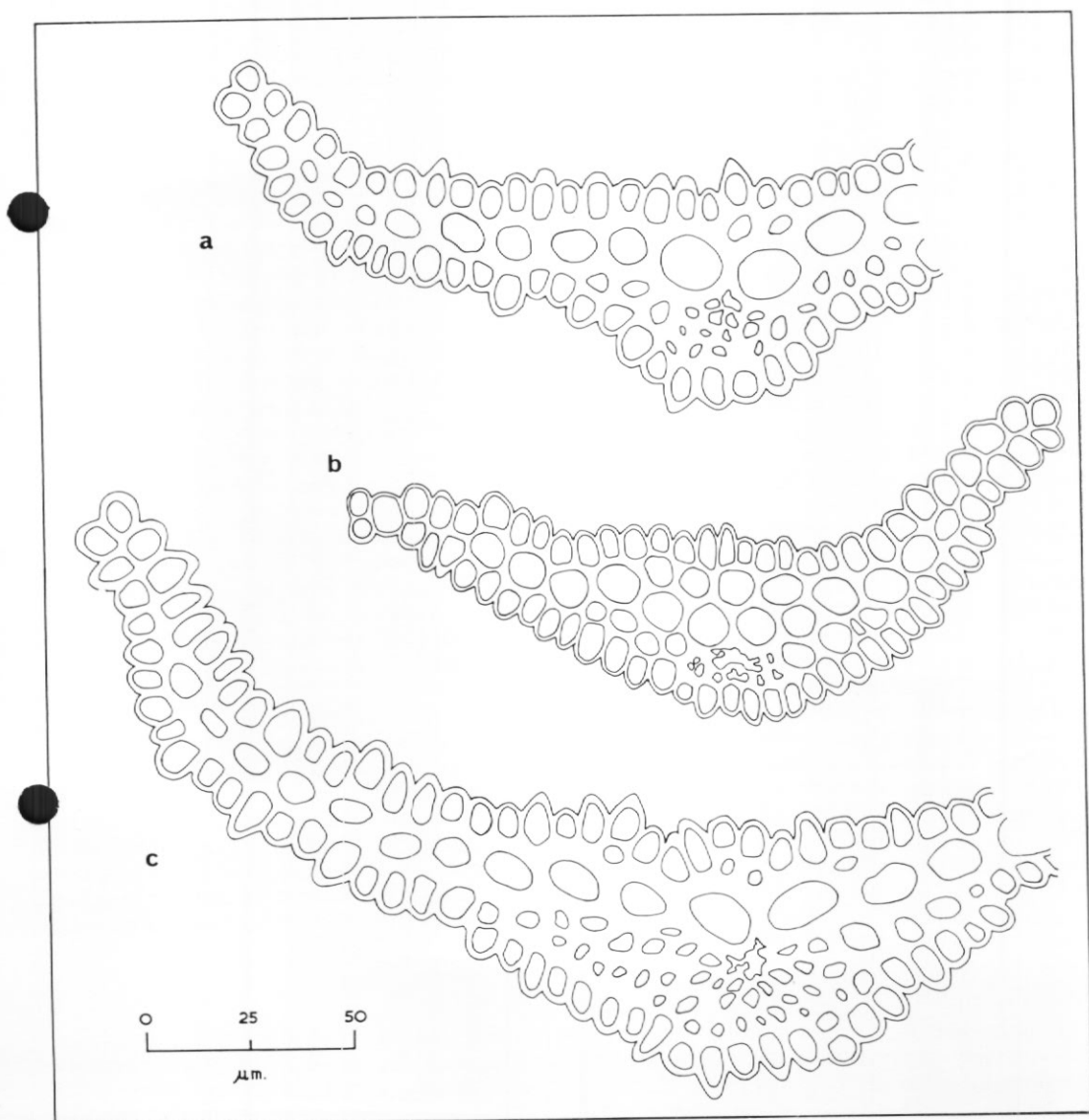


Fig. 5. Transverse sections from approximately half-way along leaf limbs of South Georgian specimens of (a) and (b) *Bartramia* group and (c) *Exodokidium* group to show variation in nerve structure.

but the boundary of nerve (E-type midrib as described by Kawai (1968)) and lamina is ill-defined, whereas the upper and lower cell layers of the nerve are continuous with and undifferentiated from the cells of the lamina. About the mid-point of the leaf a dorsal, and usually a ventral, group of very small incrassate cells is interspersed between the outer cell layer and a central row of more or less thickened large cells, which extend into the lamina for much of its width. In plants falling into the main cluster of variation in leaf dimensions (the *Bartramia* group), the diameter of these central cells diminishes conspicuously away from the mid-point of the leaf, or there is a double row, whereas they tend to be more uniform in those plants with relatively wider leaf bases and invariably form a single row (the *Exodokidium* group).

The stem section of *Exodokidium subsymmetricum* described by Cardot (1908) has been found to differ in no significant way from South Georgian specimens of the *Bartramia* group or other members of the Bartramiaceae, such as *Breutelia integrifolia* (Fig. 6). The radial and inner tangential walls of the outermost cortical cells are greatly thickened but the outer tangential walls are thin, in common with those of the inner cortex, which surrounds a central cylinder of very small cells.

Structure of capsules

Cardot (1906, 1908) distinguished the genus *Exodokidium* from *Bartramia* by its shorter, triangular-lanceolate leaves, and by the presence of transverse lamellae on the outside of the outer peristome teeth. In common with other members of the Arthrodontae, the outer peristome of the Bartramiaceae is a two-ply structure (Fig. 7a). In South Georgian representatives of *Bartramia* and *Exodokidium*, the outer layer is thin with its surface covered by fine papillae and/or striae, whereas the inner layer is considerably thickened, particularly at the articulations. Slight thickenings are, however, not uncommon in the outer layer, and are usually associated with its articulations, which differ from those of the inner layer, although thickenings may also occur longitudinally (Fig. 7b-g). These thickened parts have been observed in approximately one-third of those specimens of undoubted *Bartramia* with mature and perfect capsules, but they were rarely as well developed as was suggested by Cardot's diagram of *Exodokidium* (Cardot, 1908). In only one of four syntypes of *Exodokidium subsymmetricum* (Skottsberg 329, S-PA; Géorgie du Sud, baie Cumberland, Jason Harbour, 23.iv.1902), were such bars observed, and they were quite indistinct (Fig. 7f). This specimen was examined by Cardot, but thickenings were completely absent from the only other syntype (Skottsberg 330, S-PA) in which this character could be studied. Possible explanations for this discrepancy are that all capsules within a specimen may not be alike, or that Cardot may have observed, through the outer layer, the thickenings of the inner layer. However, it must be concluded that the feature, occurring indiscriminately in *Bartramia* and *Exodokidium*, is valueless as a diagnostic character.

The form of the capsule, to which the specific epithet *E. subsymmetricum* refers, does however afford an easily observed and constant means of distinguishing between the South Georgian *Bartramia* and *Exodokidium* groups. Thus the mature capsule of plants of the latter group is erect and almost perfectly symmetrical, becoming urceolate on drying, whereas that of the former is usually distinctly asymmetrical and, even in the dry state, invariably narrows to the orifice. Moreover, it has been found that a pronounced difference in the exothecial cells is associated with these two types of capsule. In general terms, the areolation of the outer wall of the *Exodokidium* capsule is compact and incrassate, whereas that of *Bartramia* is lax and either collenchymatous or has differentially thickened walls, the longitudinal walls being thicker than the transverse cell walls.

Status of groups

It is evident that taxonomic distinction between the small *Exodokidium* group of plants incompletely separated by leaf dimensions from the majority of *Bartramia* specimens is possible by reference to sporophyte characters. Nevertheless, a certain amount of material in the intermediate range would remain indeterminate in the absence of fruit. The validity of the two groups as well-defined taxa has been firmly established, however, by the recognition of diagnostic differences in transverse sections of leaves (Fig. 8).

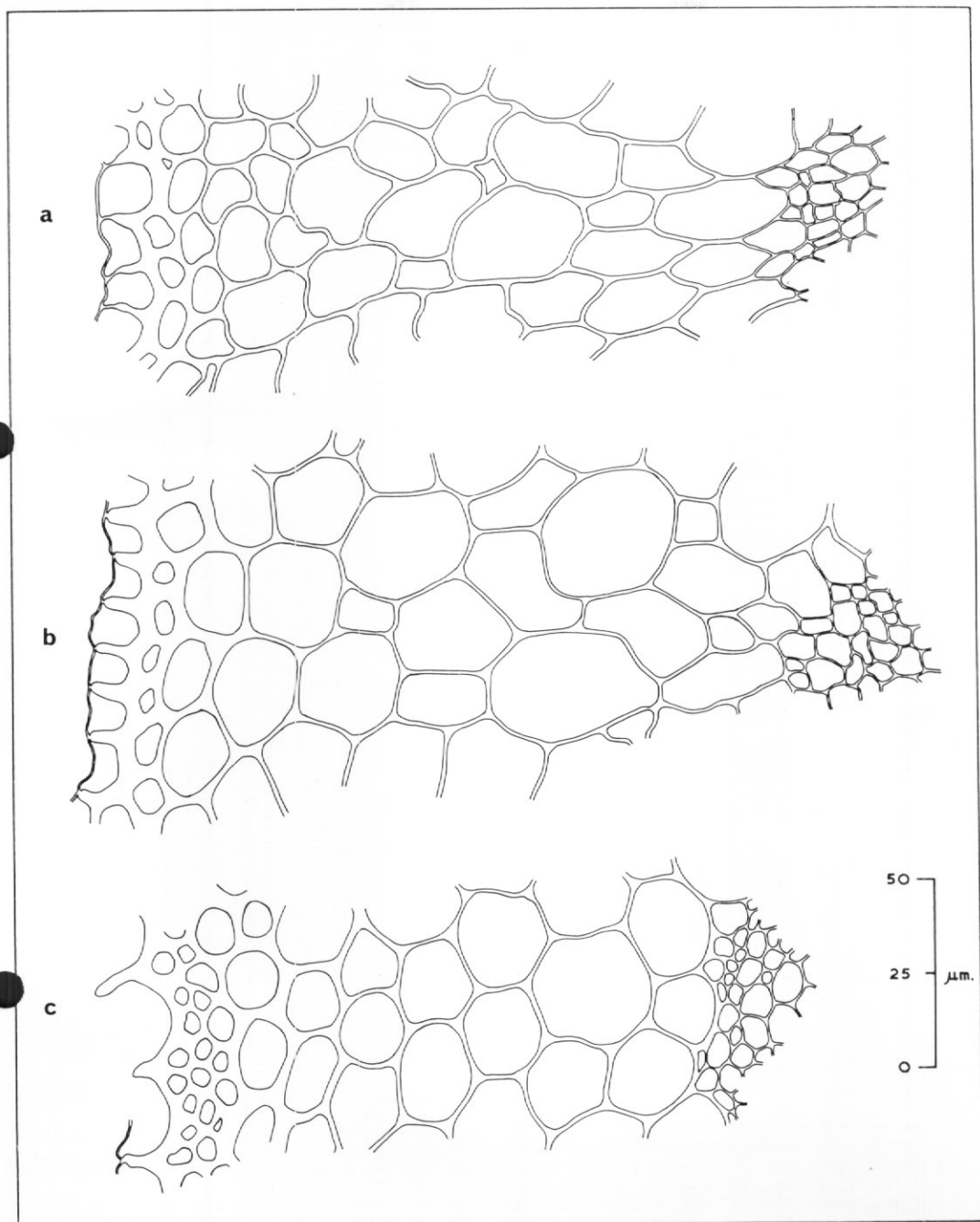


Fig. 6. Transverse sections of stems of South Georgian specimens of: a. *Bartramia* group; b. *Exodokidium* group (= *Bartramia subsymetrica*); c. *Breutelia integrifolia* (with outermost cortical cell walls ruptured) to show similarities in cell arrangement. Outer cortex to the left and central cylinder to the right.

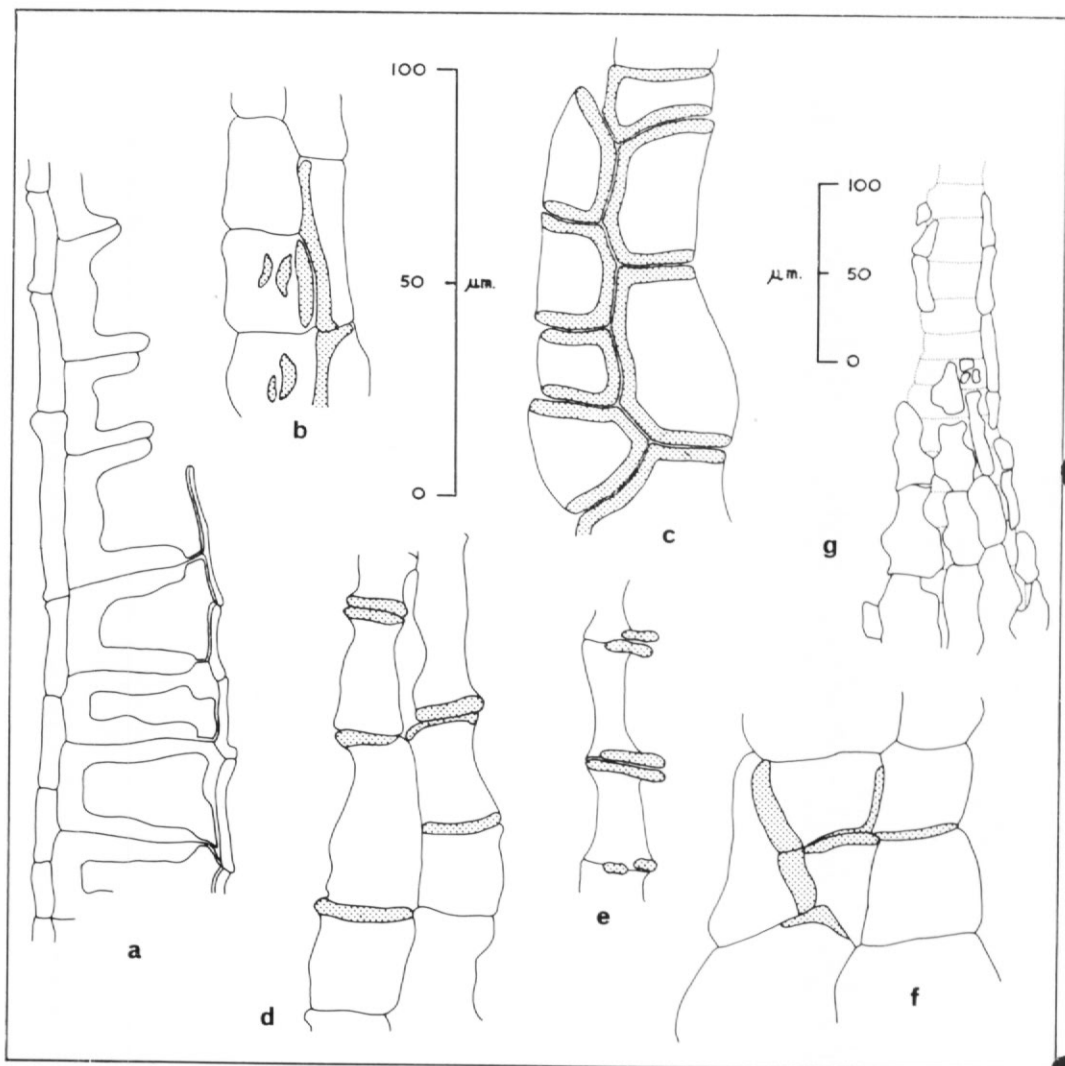


Fig. 7. Comparison of peristome structure in South Georgian specimens of *Bartramia* and *Exodokidium*.
 a. Lateral view of inner and outer peristome of *Bartramia* group. The small inner tooth (to the right) is attached to the internal trabeculae of the large outer tooth (to the left), the outer layer of which is slightly thickened at its articulations.
 b. Outer surface view of part of outer peristome tooth of *Bartramia* group with longitudinal thickenings in its outer layer.
 c. Outer surface view of part of outer peristome tooth of *Bartramia* group with thickenings at transverse and longitudinal articulations of its outer layer.
 d. and e. Outer surface view of part of outer peristome tooth of *Bartramia* group with thickenings only at the transverse articulations of its outer layer.
 f. Outer surface view of part of outer peristome tooth of *Exodokidium* group with limited transverse and longitudinal thickenings at the articulations of its outer layer.
 g. Inner view of peristome of *Bartramia* group showing rudimentary inner tooth in relation to outer tooth.
 Stipple indicates raised portions. Left-hand scale refers to a-f. Right-hand scale refers to g.

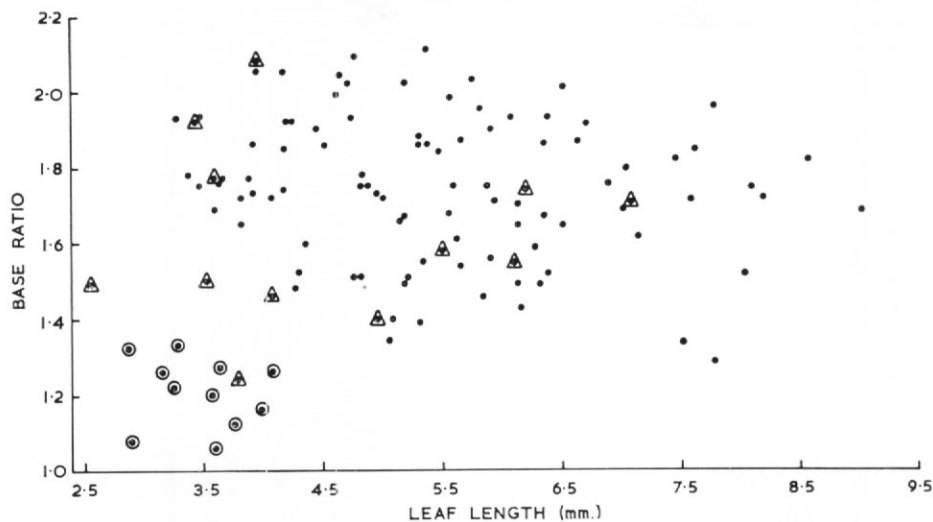


Fig. 8. Scatter diagram of distribution of a sample of *Bartramia* group leaf section (Δ) and *Exodokidium* group leaf section (\circ) in relation to base ratio (length/breadth) and leaf length in South Georgian specimens of *Bartramia* and *Exodokidium*.

Although Cardot (1908) had not seen male inflorescences, he reported that *Exodokidium subsymmetricum* was apparently dioecious, a state which the present study has confirmed. Its sexual habit, therefore, distinguishes this taxon from the majority of fertile specimens of *Bartramia*, only five out of a total of 110 being other than synoecious. In these, only female inflorescences were found. This is of particular interest as Müller (1890) described *B. leucolomacea* as dioecious, a character which would serve to distinguish it from the other species of *Bartramia* reported from South Georgia. However, two isotypes are undoubtedly synoecious, as reported by Cardot (1908) who saw one of them.

Some specimens of *Bartramia* and *Exodokidium* are difficult to determine according to growth form and habitat characters alone, but *E. subsymmetricum* is generally recognizable by its tall, rigid, densely tomentose stems with strict leaves. Plants of *Bartramia* are usually shorter and often equally tomentose, but the narrower frequently patent leaves give most of them a distinctive appearance, and few could be regarded as intermediate with respect to habit.

VARIATION IN *Breutelia*

Leaf length is only slightly correlated with leaf breadth, as shown by data derived from 60 specimens (Fig. 9), and the variation is continuous throughout its range. Conversely, leaf ratio is strongly correlated with the limb/base ratio, but marked discontinuity isolates plants with narrow leaves and relatively long fine apices from others with shorter and broader leaves (Fig. 10). However, it is considered that this separation is not of taxonomic significance because detailed examination of a wide variety of gametophyte characters failed to reveal any other differences between the two groups. Moreover, the isolated group was heterogeneous with respect to leaf length and leaf breadth. It is believed that measurement of a further series of specimens would eliminate this discontinuity and it would therefore appear that the genus is restricted to a single taxon on South Georgia, thus confirming all previous records.

IDENTITY OF SOUTH GEORGIAN TAXA

In accordance with the evidence presented above, three taxa can be recognized. One small group of specimens corresponds with Cardot's *Exodokidium subsymmetricum*, the remaining two groups comprising very variable material, one conforming to *Bartramia patens* and the other to *Breutelia integrifolia*. The range of variation in South Georgian *Bartramia patens* is very great and accounts for the large number of taxa reported on the basis of a comparatively

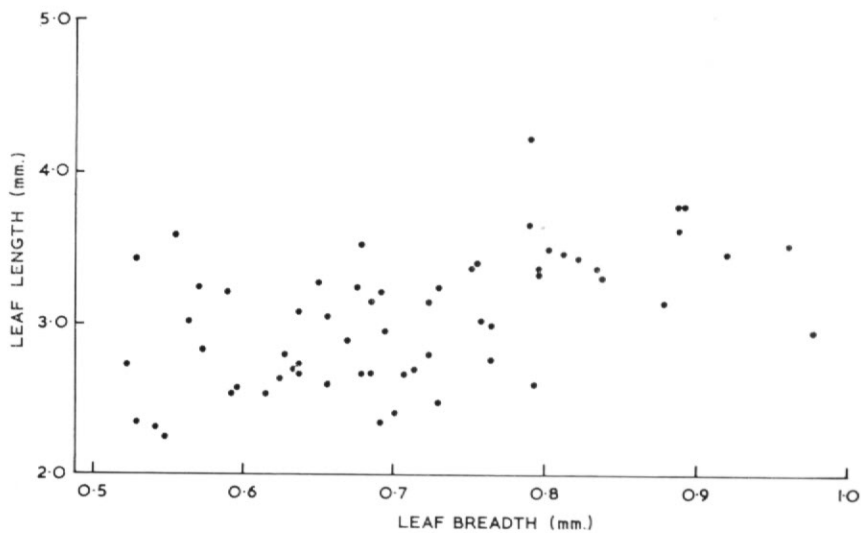


Fig. 9. Scatter diagram of variation in leaf length and breadth in South Georgian specimens of *Breutelia*.

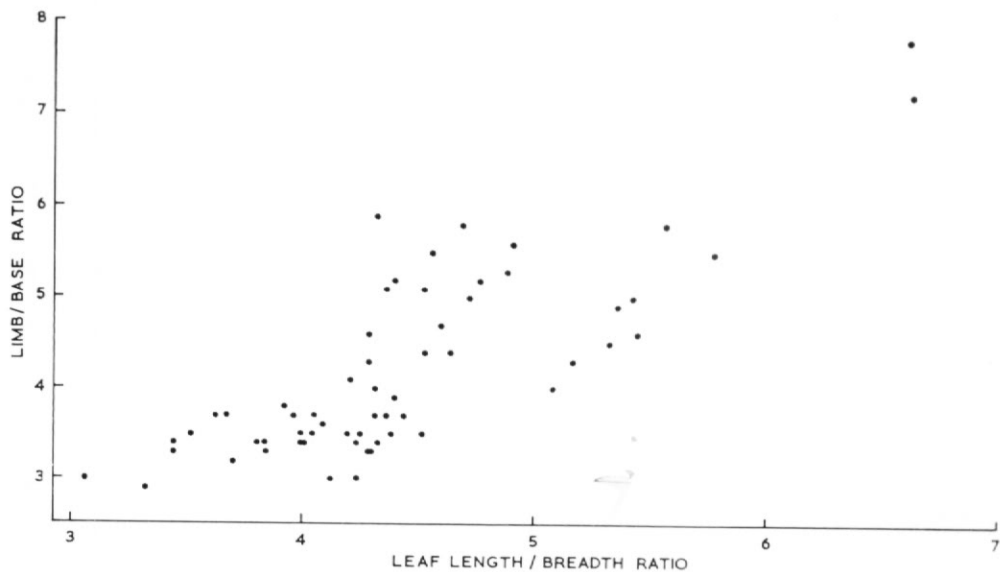


Fig. 10. Scatter diagram of variation in the ratio of limb/base (a/b ratio) and leaf length/breadth ratio in South Georgian specimens of *Breutelia*.

small number of gatherings from which the continuity of variation could not be appreciated. A smaller range in each of the other two taxa has not led to such a proliferation of species.

Bartramia patens was described as tending to be yellowish in colour and with capillaceous, spreading entire leaves (Bridel, 1803). This last character has long been regarded as merely the outcome of superficial examination. Müller (1849), for example, described the leaf margin as sparingly dentate and this is in accordance with the type specimen (B: E fret Magellanico Commerson, retulit, Tortain & Ousndu Island, 1797) described by Bridel (1803). Its leaf dimensions are well within the range of variation recorded on South Georgia. The only capsule present appears to be erect, as described by Bridel, but it is considered that this is because it has been pressed in the only plane of symmetry. A description of the peristome was not, however, included by Bridel, and as a consequence a small form was later described as *B. subpatens*, said to be distinguished by its imperfect inner peristome (Müller, 1890). Nevertheless, the inner peristome of all the South Georgian *Bartramia* specimens examined, during the present study has been observed to be more or less rudimentary and attached to the outer peristome teeth (Fig. 7a and g). Cardot (1906) considered this species to be no more than a form of *B. patens* and included it in f. *austrogeorgica*. It is of interest that, although material of both *B. subpatens*, as shown by the isotype (Will, HBG; Fundort Whalerbay, Süd-Georgien, 30.xi.1882) (Müller, 1890), and *B. patens* f. *austrogeorgica*, as shown by the first South Georgian specimens (Skottsberg 339, S-PA; South Georgia, Cumberland Bay, 400–500 m.s.m. in monte supra Pot Harbour, 21.v.1902; Skottsberg 338, S-PA; South Georgia, Cumberland Bay, valley between south and west fiords, 21.v.1902) (Cardot, 1908), falls within the range of variation in the single taxon of *Bartramia* on South Georgia, their leaf dimensions were not found to be in close proximity. The leaves of the two latter specimens are very small and not, therefore, closely related to the type material of *B. subpatens*. Cardot (1906) also described *B. patens* f. *chrysocolea* with less widely spreading leaves and yellow leaf bases and *B. patens* f. *fragilifolia* in which the leaves were easily broken. The leaves of the type specimen of the latter (Skottsberg 333, S-PA; South Georgia, Royal Bay, Moltke Harbour, 27.iv.1902) (Cardot, 1908) have very fine limbs and fall outside, or at the limits of, the variation included in Figures 1 to 4, but the dimensions of the former (Skottsberg 332, S-PA; South Georgia, Cumberland Bay, Jason Harbour, 23.iv.1902) (Cardot, 1908) are not unusual in this respect.

It has been confirmed that the small group of plants which includes the type material of *Exodokidium subsymmetricum* (Skottsberg 328, 329, 330, S-PA), with relatively broader leaves than most specimens of *Bartramia patens*, can be recognized as a distinct taxon. Only its compactly caespitose growth form, taken in conjunction with leaf shape and capsule shape, remains to afford any means of taxonomic recognition after critical assessment of the characters considered by Cardot (1906) to be diagnostic of *Exodokidium*. To these can now be added characters based on exothelial areolation and nerve structure. Nevertheless, it is considered that there is insufficient distinction to justify recognition at generic level as all of the characters, with the possible exception of exothelial cell structure, are modifications of very similar organs and tissues in species of *Bartramia*. It is therefore proposed to return *Exodokidium subsymmetricum* to the genus *Bartramia*, as *B. subsymmetrica*.

Variation within the single species of *Breutelia* on South Georgia has been compared graphically with the first specimen of *B. kerguelensis* (Par.) Wijk & Marg. reported from the island as *Breutelia graminicola* (C. Muell.) Broth. & Card. (*nom. illeg.*). Cardot (1906) compared this material (Skottsberg 363, S-PA; Géorgie du Sud, Cumberland Bay, Bore Valley, 7.v.1902, ex herb. H. J. Möller) to Müller's type specimen from Iles Kerguelen, but it clearly lies within the range of variation displayed in Figs. 9 and 10.

Breutelia kerguelensis is one of a group of four species with entire leaves included in the section *Acoleos* by Brotherus (1904), to which *Breutelia skottsbergii* Card. (Cardot, 1905) may be added. The first to be described (Taylor, 1846) was *B. integrifolia* (Tayl.) Jaeg., of which three specimens from the *locus classicus* in Equador (BM; Jameson 40, Andes of Quito, ex herb. G. J. Lyon; Jameson 40, Andes of Quito, ex herb. R. J. Shuttleworth; R. Spruce 398, Andes Quitans in Monte Pichincha ad cataractam, 11,000 ped., det. Mitten) have been examined and found to fall within the scatter of variation of every character studied in the South Georgian material. Similarly, two specimens, one an isotype, from the type locality of *Bartramia mniocarpa* C. Muell. (BM; Bolivia-Regio Guaylloputonia, 3,500 metr., mis.

Schimper, ex herb. Hampe; Guaylloputoneo, Bolivia, 10,000', leg. Mandon, ex herb. Hampe), which was regarded as synonymous with *Breutelia integrifolia* by Hampe (*in sched.*), were also found to fall within this range of variation. Hence *Bartramia mniocarpa* C. Muell. is here reduced to synonymy with *Breutelia integrifolia*. Schimper (1897) used the *nomen nudum*, *Bartramia mniocarpa*, as recorded by van der Wijk and others (1959) but Müller (1897), by providing a description and a reference to the original specimen, validated the name as *Bartramia (Breutelia) mniocarpa* C. Muell. According to Paris (1900), *Bartramia mniocarpa* Schimp. (*nom. nud.*) is synonymous with *Breutelia macrocarpa* Schimp.

The type description of *Breutelia kerguelensis* is inadequate and the only character distinguishing this species from *B. integrifolia* would appear to be its spreading leaves, as opposed to the erecto-patent leaves of the latter. Both types of leaf arrangement occur in South Georgian material of *Breutelia*, not only in specimens with ovate-lanceolate leaves, such as those reported in *B. integrifolia*, but also in those with ovate leaves. In addition, a single twist towards the leaf apex, which has been said to be usual in *B. integrifolia* (Taylor, 1846), has been observed in several gatherings from South Georgia but it is not present in the leaf illustrated by Brotherus (1904). It is therefore considered that recognition of two species on South Georgia is not justifiable. Further work is necessary to determine whether *B. kerguelensis* has any validity, since two isotypes of *Bartramia graminicola* (Naumann, H; Kerguelen, ex herb. V. F. Brotherus; Naumann, Kerguelen, ex herb. V. F. Brotherus, *Bartramia (Philonotis) graminicola* (C.M.) Broth., Lectotype! det. C. M. Matteri, 1971) fall outside the scatter of variation known in South Georgian material, although their leaf proportions are not exceptional.

STATUS OF RELATED TAXA

For the purposes of taxonomic discussion, the leaf dimensions of type specimens of the taxa recognized on South Georgia have been plotted in the scatter diagrams (Fig. 11), although the first specimen of *B. diminutiva* reported from the island was substituted for the type, which has been lost. This specimen was identified by Cardot, who had seen Müller's type specimens. Similarly, the type specimen of *B. oreadella* has been destroyed but two isotypes from the *locus classicus* obtained 3 days previously by the same collector, and seen by Müller, have been examined. Because type material was limited, some of the values for these specimens had to be based on smaller samples than the remainder but in each case the measurements are considered adequate for drawing conclusions.

Bartramia diminutiva, a small form with erect leaves, was described from Iles Kerguelen (Müller, 1883) and Cardot (1906) recognized it as a South Georgian species. The type specimen (Ins. Kerguelen, Winter Harbour, 13.i.75) has been lost but a specimen from South Georgia (Skottsberg 346, S-PA; South Georgia, Cumberland Bay, Pot Harbour, 15.v.1902), which was identified by Cardot (1908) on the basis of comparison with Müller's type specimen, has been studied. Whilst lying within the defined variation of *B. patens*, both its leaf length and leaf breadth are amongst the smallest recorded. *B. diminutiva*, in common with *B. leucolomacea* and *B. oreadella*, has been described as glaucous-green in colour, a colour which occurs throughout the range of *Bartramia* on South Georgia.

A correct interpretation of Müller's (1890) description of a thick-walled capsule in *Bartramia oreadella* remains obscure. Müller's herbarium at Berlin Dahlem has been lost and with it the type specimen of *B. oreadella* (Austro-Georgia, in fissuris rupium des oberen Whalerthal, 23 Martio 1883, fructibus maturis). In the absence of known isotypes, two named specimens with collecting details that are identical with those of the type specimen, apart from the date, have been examined. These specimens (Will, HBG, M; Oberes Whalerthal in Felsspalten, Süd-Georgien, 20.iii.83) are clearly *B. patens* and suggest that an exothecial wall similar to that of *Exodokidium subsymmetricum* may not have been implied. The longitudinal cell walls are thicker than the transverse walls but it has not been possible to associate the two types of exothecial cells with any other character.

The white margin of the leaf base in *B. oreadella*, considered of diagnostic importance by Müller (1890), is of very frequent occurrence in South Georgian material, and Cardot (1908) pointed out its presence in the original specimens of *B. pycnocolea*, *B. diminutiva* and *B. patens*. Together with its variety *microphylla*, *B. oreadella* is not exceptional in the variation observed

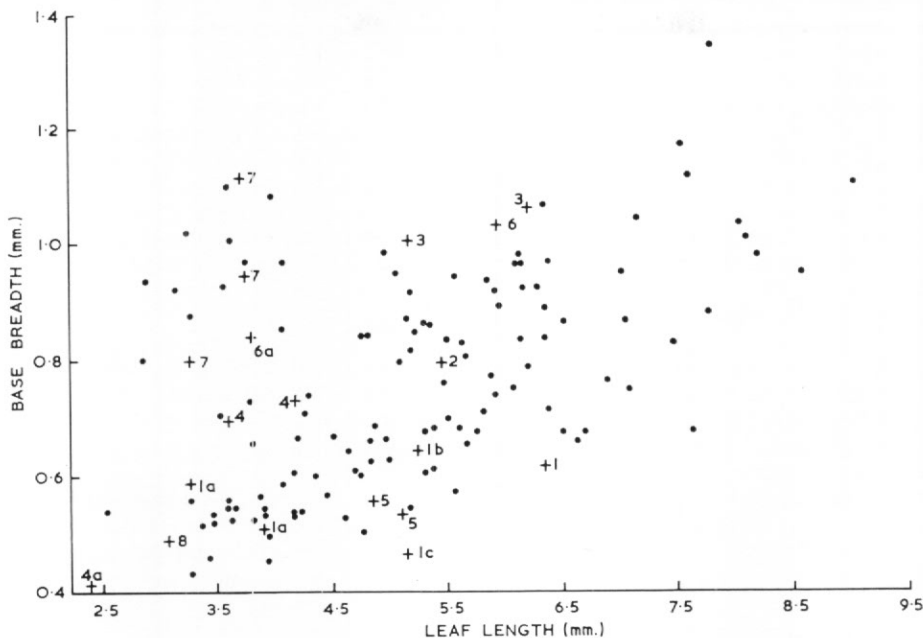


Fig. 11. Scatter diagram of variation in base breadth at widest point and leaf length in South Georgian specimens of *Bartramia patens* and *B. subsymmetrica* with the relative positions of type specimens (1-7) of species of *Bartramia*.

1. *Bartramia patens* Brid.; 1a. *B. patens* f. *austrogeorgica* Card.; 1b. *B. patens* f. *chrysocolea* Card.; 1c. *B. patens* f. *fragilifolia* Card.; 2. *B. subpatens* C. Muell.; 3. *B. leucolomacea* C. Muell.; 4. *B. oreadella* C. Muell.; 4a. *B. oreadella* var. *microphylla* Card.; 5. *B. pycnocolea* C. Muell.; 6. *B. leucocolea* Card.; 6a. *B. leucocolea* var. *brevifolia* Broth. & Card.; 7. *B. subsymmetrica* Card.; 8. *B. diminutiva* C. Muell.

during the present study, although type material of the former, as well as specimens from the *locus classicus* of the latter, are amongst representatives of the smallest leaf dimensions in *B. patens*. *B. oreadella* var. *microphylla* Card. was apparently considered to be very close to *B. diminutiva*, as shown by reference to the type specimen (Skottsberg 15 *in parte*, S-PA; Tierra del Fuego, in monte supra Ushuaia, reg. alpina, 11.iii.1902) (Cardot, 1905); it is here referred to *B. patens*.

Bartramia pycnocolea, distinguished from all other species of South Georgian *Bartramia* by its appressed leaves and soft bi-coloured stems (Müller, 1890), falls entirely within the variation of *B. patens*, known from South Georgia (Figs. 1-4), and cannot therefore be considered as distinct. Its two isotypes (Will, HBG, M; Felsen im Hochthal über dem oberen Whalerthal, 160 mtr. über dem Whalerthal, Süd-Georgien, 18.iii.83) (Müller, 1890) are amongst plants with leaf breadth towards the lowest limit recorded.

Isotypes of the destroyed syntypes of *Bartramia leucolomacea* (Will, HBG; Hochplateau, Auf trockenem, steinigem Boden, Süd-Georgien, 23.i.83; Köppenberg, an Felsen, Süd-Georgien, 18.i.83), reported to be dioecious (Müller, 1890), have been found to be synoecious and their more or less secund leaves with a pale margin to the limb occur to a greater or lesser extent throughout the entire range. This is in accordance with Cardot's (1908) observation that plants with homomalous leaves, which thus coincide with *B. leucolomacea*, not uncommonly had only a poorly developed pale leaf margin.

Leaf dimensions in *B. leucolomacea*, a species which has been considered to be possibly no more than a form of *B. patens* (Cardot, 1908), have been measured in the two isotypes. Their leaves are wide but are included within the limits for *B. patens*, and are almost identical with those of the type specimen of *B. leucocolea* (Skottsberg 104, S-PA; Tierra del Fuego, Ushuaia, in litore, 18.iii.1902) (Cardot, 1908), a species which has also been reported on South Georgia (Cardot, 1908).

Plants with widely spaced leaves and conspicuous white leaf bases have been described as *B. leucocolea* (Cardot, 1905). The leaves were reported to be shorter than those of *B. patens* but also larger and, by plotting values obtained from the type specimen in the scatter diagrams, it was found that leaf width was at the upper limit of the variation shown by that character. Gatherings that would coincide with *B. leucocolea* var. *brevifolia* Broth. & Card., as shown by the type specimen (Skottsberg 50, S-PA; Géorgie du Sud, baie Cumberland, Moraine fiord, prairies, 1909, ex herb. H. J. Möller) (Cardot and Brotherus, 1923), are of particular interest because they have short broad leaves, and are therefore those most likely to be confused with plants identified as Cardot's *Exodokidium subsymmetricum*. Exothelial cell structure and the structure of the nerve in transverse section show clearly, however, that they are referable to *B. patens*.

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